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ON THE UPPER JURASSIC ICHTHYOSAUR REMAINS FROM THE RUSSIAN NORTH

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ABSTRACT

An ichthyosaurian skeletal remains assigned to the genera *Arthropterygius* and *Ophthalmosaurus* are described from the Volgian deposits of the Komi Republic and Nenets Autonomous Region (Okrug) (Russia). These specimens along with findings from Svalbard provide an opportunity to draw some preliminary conclusions on the distribution of ichthyosaurs during the Late Jurassic and Early Cretaceous epoch.

Key words: *Arthropterygius*, ichthyosaurs, *Ophthalmosaurus*, Russia, Upper Jurassic

ОБ ОСТАТКАХ ИХТИОЗАВРОВ ИЗ ВЕРХНЕЮРСКИХ ОТЛОЖЕНИЙ РУССКОГО СЕВЕРА

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РЕЗЮМЕ

Остатки ихтиозавров, отнесённые к родам *Arthropterygius* и *Ophthalmosaurus*, описаны из волжских отложений Республики Коми и Ненецкого автономного округа (Россия). Наряду с находками из Шпицбергена они позволяют предварительно наметить пути расселения ихтиозавров в позднеюрскую и раннемеловую эпохи.

Ключевые слова: *Arthropterygius*, ихтиозавры, *Ophthalmosaurus*, Россия, верхняя юра

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INTRODUCTION

Hitherto just a few ichthyosaur vertebrae from the Timan-Pechora Jurassic deposits have been described (Riabinin 1912). However, the important specimens from this area still have not been studied. In 2013, the authors conducted a study of the Mesozoic marine reptile remains deposited at the Vernadsky State Geological Museum of Russian Academy of Sciences (Moscow, Russia). Among these specimens an association of ichthyosaurian bones were detected. This material was collected by famous Soviet geologist and paleontologist Vladimir Vasil'evich Menner near the Porozhsk village (Sosnogorsk District, Komi Republic) (Fig. 1) in 1943–44 (Fishman 1999). The tag of this specimen does not contain the detailed information on the stratigraphic range. There was only noted the Upper Jurassic age of these bones. Fortunately, two vertebrae from this collection were partly covered by blackish clay, which contained an assemblage of ostracods, foraminifers and dinoflagellate cysts. All these microfossils indicate the Volgian age (see Appendix). The Upper Jurassic section crops out near the Porozhsk village along the Izhma River banks is typical for the area. Its upper part is represented by the Middle Volgian oil shale and clay members of Paromes Formation (Kravets et al. 1976) (Fig. 2).

Another material represented by an incomplete ichthyosaur forefin was collected in 2013 by one of the authors (P.A.B.) during the field works in the Polar District of Nenets Autonomous Region (Okrug). The specimen was found in a scree of Mesozoic outlier, encased into the Quaternary fluvioglacial deposits. The outlier is located on the right bank of the river Volonga, 7 km above the mouth (GPS-coordinates: 67°06'55''NL, 47°51'46'' WA) and stretches for 20 m below and 100 m above the Chasovenny creek (Fig. 1). The section is composed of darkish silts and clays with a total thickness of nearly 5 m and divided into the Middle and Upper Volgian and Berriassian beds (Beznosov 2013) (Fig. 2).

The specimen was partially enclosed into the mudstone nodule. The bones were coated with consolidant 'Paraloid B-72' in an acetone solution. After drying, the matrix was dissolved by using warm 10% acetic acid solution. After the preparation, the mud sludge was precipitated. It contained abundant and poorly preserved microphytobenthos. The observed miospore assemblage is typical for the Volgian Stage.

However, the presence of two Cretaceous species (*Leberidocysta* sp., *Aptea anaphrissa* (Sarj.) Sarj. et Stover) does not allow us to precisely determine the specimen's stratigraphic range (see Appendix 1).

The study of the skeletal remains from the Vernadsky State Geological Museum allows us to assign them to the genus *Arthropterygius*, whose members are also known from the Upper Jurassic of Canada and Argentina (Fernández and Maxwell 2012; Maxwell 2010; Russell 1993). According to Maxwell (2010, p. 404), one of the diagnostic characters of *Arthropterygius* is the opening of the internal carotid foramen located on the posterior part of the basisphenoid. The humerus has three deeply concave distal facets, the humeral "torsion" is slight; deltopectoral crest is extremely reduced and shifted anteriorly. Furthermore, in *Arthropterygius* the facet for the basioccipital on the basisphenoid faces posterodorsally, while it faces posteriorly in other ophthalmosaurids (Kear 2005; Kirton 1983; McGowan and Motani 2003; Fischer et al. 2011, 2012). These features are likewise present in skeletal remains SGM 1502, described in this publication. However, our study demonstrates that the morphology of bones stored in the SGM, shows some differences as compared to the previously known specimens of the genus. It is important to note that humeral morphology of SGM 1502 is very similar to recently erected *Janusaurus lundi* Roberts et al., 2014, the only difference being the presence of muscular tubercles. However, the state of preservation of the *J. lundi* basisphenoid does not allow us to provide a more detailed comparison (Roberts et al. 2014).

The incomplete forefin from Nenets Autonomous Region has been determined as *Ophthalmosaurus* sp. based on the following anatomical features: three distal articular facets of the humerus for the radius, the ulna, and the anterior accessory element; the margin of the anterior distal facet is sub-triangular in shape (the autapomorphic feature of *Ophthalmosaurus*); the ventral torsion of the ulnar facet is absent (Andrews 1910; Kirton 1983; McGowan and Motani 2003).

Thus, the ichthyosaur specimen from the Porozhsk site reveals additional characteristic features for the genus *Arthropterygius*. Both new finds from northern Russia have an obvious palaeobiogeographical significance due to the recently established taxonomic resemblance of ichthyosaurian associations from the Norway, Russia, UK, Canada, Chile and Argentina (Fernández and Maxwell, 2012; Pardo Pérez et al. in press; J.P.P. unpublished data). This suggests that



Fig. 1. Map of northern European Russia showing the ichthyosaur discovery sites. Localities are marked by an asterisk. 1 – *Arthropterygius* sp. (SGM 1502); 2 – *Ophthalmosaurus* sp. (IG KSC-415/38).

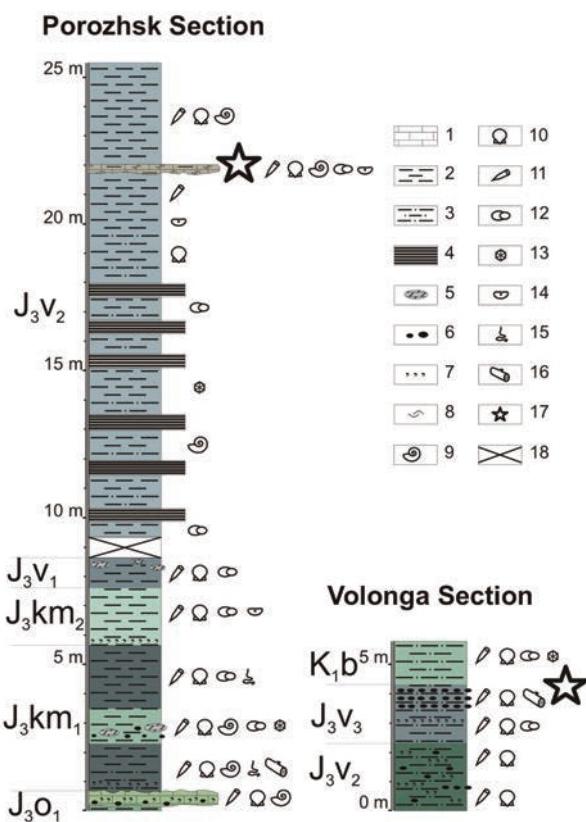


Fig. 2. Lithological logs of Porozhsk and Volonga sections: 1 – limestones; 2 – clay; 3 – aleurite; 4 – bituminous shales; 5 – marly concretions; 6 – phosphorite nodules; 7 – glauconite; 8 – coquina; 9 – ammonites; 10 – bivalves; 11 – belemnites; 12 – foraminifera; 13 – radiolaria; 14 – ostracods; 15 – trace fossils; 16 – remains of coalified wood; 17 – estimated levels of ichthyosaur remains finds; 18 – absence of exposure.

some ichthyosaurian taxa were preferably inhabited in the high latitude areas under the cold water conditions and also makes it possible to provide a preliminary conclusion on the faunal interchanges during the Late Jurassic and Early Cretaceous Epoch.

Institutional abbreviations. CMN, Canadian Museum of Nature, Ottawa, Canada; SGM, Vernadsky State Geological Museum of the Russian Academy of Sciences, Moscow, Russia; GIN, Geological Institute of the Russian Academy of Sciences, Moscow, Russia; IG KSC, Institute of Geology of Komi Science Centre of Ural Branch of the Russian Academy of Sciences, Syktyvkar, Russia; MOZ, Museo Prof. J. Olsacher, Dirección Provincial de Minería, Zapala, Argentina.

SYSTEMATICS

Order Ichthyosauria de Blainville, 1835

Family Ophthalmosauridae Baur, 1887 *sensu* Fischer et al., 2012

Genus *Arthropterygius* Maxwell, 2010

Type species. *Arthropterygius chrisorum* (Russell, 1993).

Distribution. Melville Island, Northwest Territories, Canada (type locality); Pampa Tril, Neuquén province, Argentina; Porozhsk village, Sosnogorsk District, Komi Republic, Russia (Fig. 1).

Stratigraphic range. Upper Jurassic. Ringnes Formation (Oxfordian to Kimmeridgian); Vaca Muerta Formation (Tithonian); Paromes Formation (Middle to Upper Volgian (Tithonian)).

Arthropterygius sp.

Referred material. SGM 1502, the partial parabasisphenoid, the rostral fragment of the snout (both the premaxilla and the dentary) with teeth, the partial mandible, three anterior trunk centra, one posterior trunk or anterior caudal centrum and one anterior caudal centrum, the medial part of the right scapula, the distal part of the right humerus.

Locality. Porozhsk village, Sosnogorsk District, Komi Republic, Russia.

Horizon. Paromes Formation, Dorsoplanites panderi Zone, Middle Volgian, Upper Jurassic.

Description. Measurements taken on SGM 1502 can be found in Table 1.

Basisphenoid. The basisphenoid is a massive bone pentagonal in lateral view and trapezoidal in dorsal view. The dorsal surface of the bone is pitted, it bears a median furrow over its entire length (Fig. 3C, D, I, J). The posterior half of the dorsal surface of the basisphenoid bears a rounded deeply pitted facet for the basioccipital (Fig. 3C–F). The ventral surface of the basisphenoid is pentagonal in outlines. It bears a large rounded facet for the articulation with the medial lamella of the pterygoid (Fig. 3A, B). The basisphenoid-parasphenoid suture is not visible. The basipterygoid processes are directed anterolaterally and partially broken. On the lateral surfaces of the basisphenoid, posterior to the basipterygoid processes, there are large pentagonal stapedial facets, which have a rough surface (Fig. 3E, F). The opening

Table 1. Measurements (mm) of SGM 1502 and IG KSC-415/38.

Element	Length	Width	Height
<i>Arthropterygius</i> sp. SGM 1502			
Basisphenoid	81	anterior – 102 posterior – 72	67
Centra			
3 anterior dorsal	35	preserved 62	87
4 or 5 anterior dorsal	35	73	80
Anterior dorsal	35	75	80
Posterior dorsal/anterior caudal	36	90	98
Caudal	33	104	102
Scapula	preserved – 152	medial expansion – 140	–
Humerus			
General proportions	preserved – 107	distal end – 147 diaphysis – 102	–
Facet for the preaxial accessory element	35	32	–
Facet for the radius	58	48	–
Facet for the ulna	60	37	–
<i>Ophthalmosaurus</i> sp. IG KSC-415/38			
Humerus			
General proportions	preserved – 105	distal end – 168 diaphysis – 107	–
Facet for preaxial accessory element	44	41	–
Facet for the radius	70	65	–
Facet for the ulna	76	67	–

for the internal carotid foramen is located in posteroventral part of the basisphenoid. It is surrounded by smooth narrow torus. The anterior surface of the basisphenoid is bordered posteriorly by the vertical wall of the dorsum sellae. The anterior foramen for the internal carotid artery is located close to the ventral surface. It is pear-shaped (narrow part is facing dorsally) (Fig. 3G, H). On either side lateral to the foramen there are pits, hypothesized by Kirton (1983) as the point of origin of an eye muscle (Fig. 3E–H). The sella turcica located in the anterior part of the basisphenoid is almost completely broken.

Premaxilla. A rostral part of the snout is preserved. It is presented by the fragments of the premaxilla and the dentary. The jaws are in occlusion, slightly macerated. The tip of the rostrum is down-turned and beak-like. Preserved length of the snout is 123 mm. On the lateral sides of the premaxilla there is a series of perforations, turning posteriorly into the continuous groove that is 3 mm wide (Fig. 4A).

Mandible. An insignificant fragment of the right mandibular ramus is preserved. It is presented by

articulated fragments of angular and surangular. Its preserved length is 150 mm. The dentary preserved in the rostral part of the snout bears a deep fossa dentalis along its lateral side (Fig. 4 B).

Dentition. Thirty-two teeth are preserved and most of them are only roots. The crowns are conical and sharply pointed. Each crown is ornamented by delicate longitudinal striations, flattening towards the apex. The height of the preserved crowns varies between 10 to 12 mm. The base of the crown is slightly bulbous. Just below the crown, each tooth exhibits a smooth area of acellular cementum that is 3.5 mm in height (Fig. 4C). Roots are circular in cross-section. Towards their base, the roots are slightly expanded and slightly curved lingually. This area shows a smooth surface with fine and longitudinal folds in the base (Fig. 4C).

Axial skeleton. For descriptive purposes we accept definitions, used by Kirton (1983) as the once of McGowan and Motani (2003) for the different regions of the vertebral column.

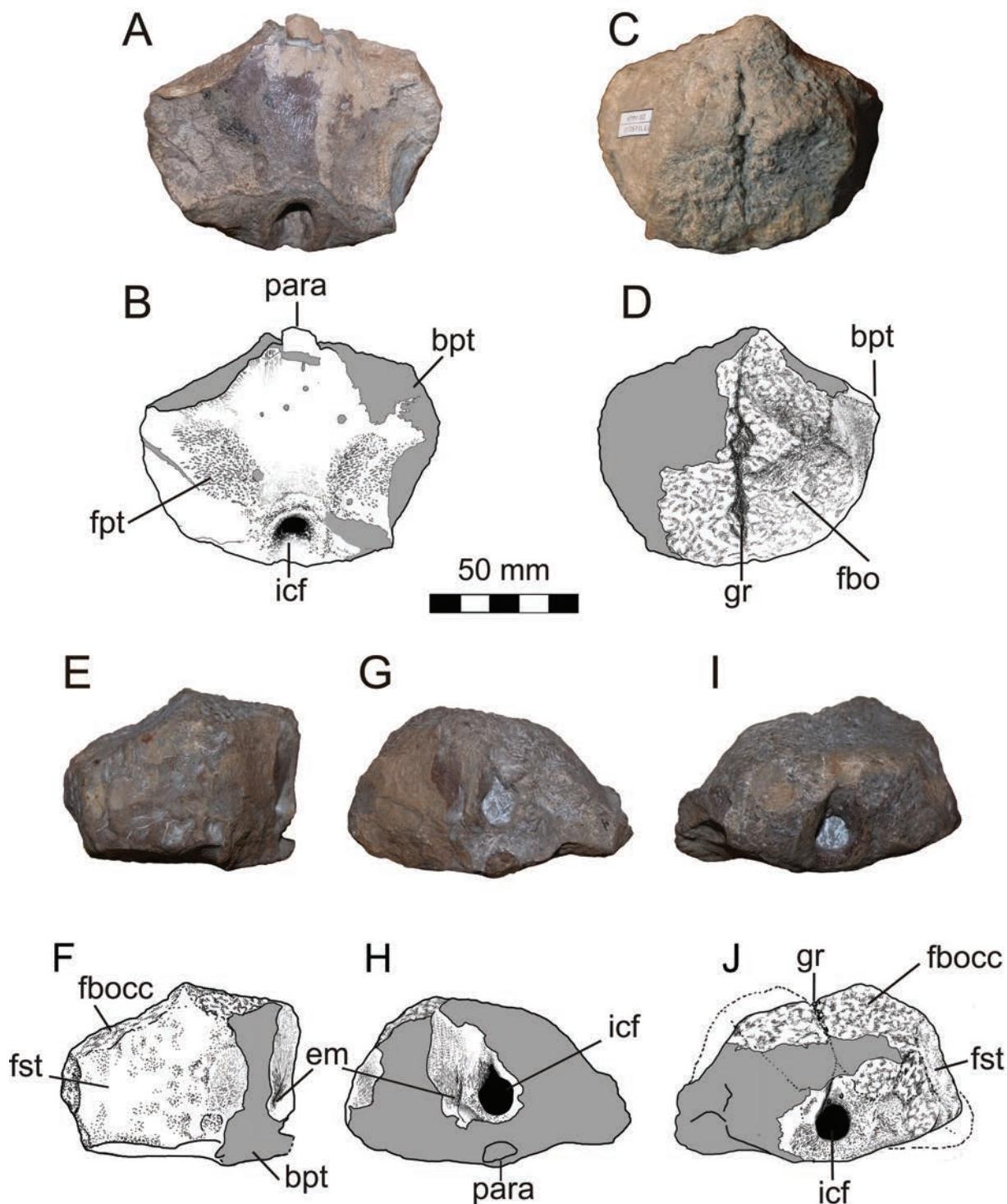


Fig. 3. Basisphenoid of *Arthropterygius* sp. (SGM 1502): A – dorsal view; B – ventral view; C – lateral view; D – anterior view; E – posterior view. Abbreviations: bpt – basipterygoid process; em – pit for origin of eye muscle; fbocc – facet for basioccipital; fpt – facet for articulation of the pterygoid; fst – facet for stapes; gr – median groove; icf – foramen for internal carotid artery; para – parasphenoid.

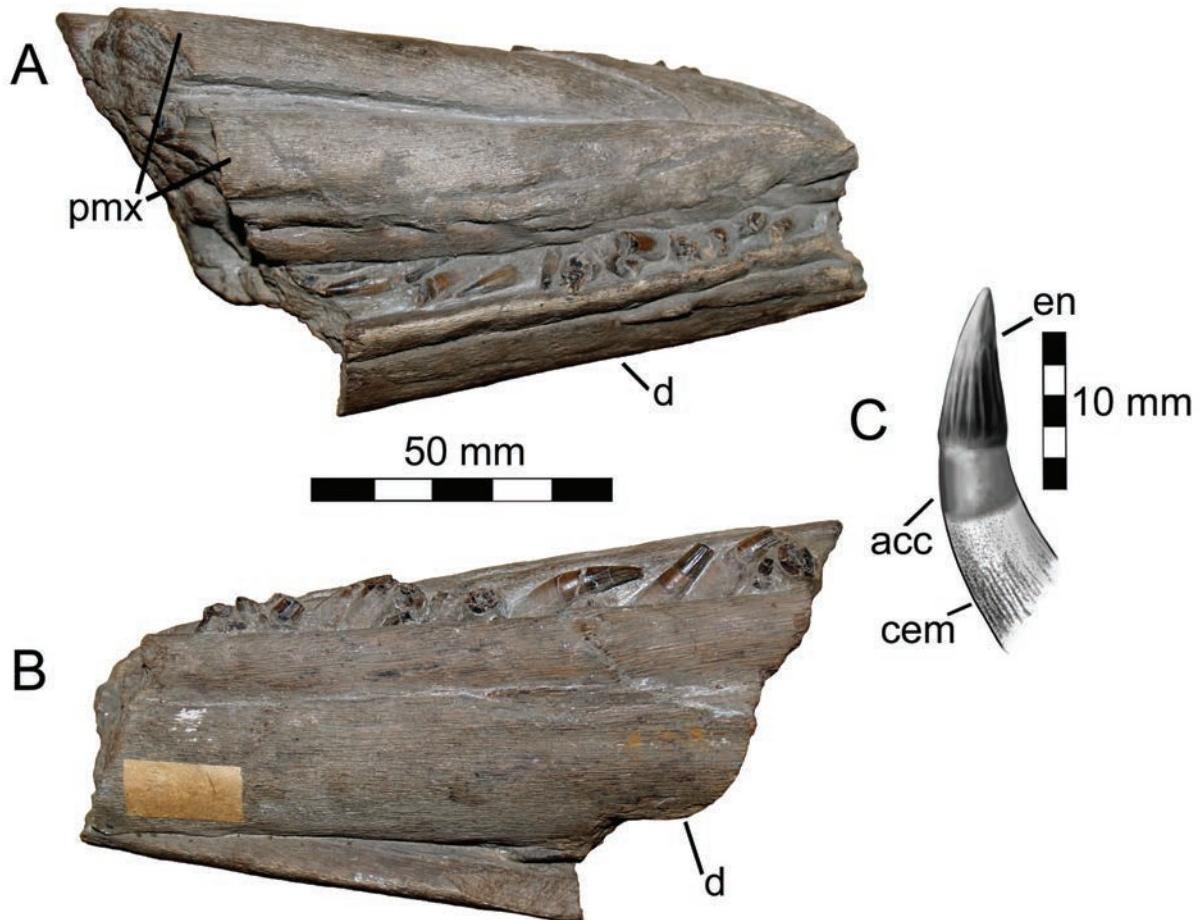


Fig. 4. Rostral part of the snout of *Arthropterygius* sp. (SGM 1502): A – dorsal view; B – ventral view; C – tooth. Abbreviations: acc – acelular cementum; cem – cementum-covered tooth base; en – enamel-covered crown; d – dentale; pmx – premaxilla.

Five centra are preserved. Three of them belong to the anterior trunk region, having diapophyses fused to the facet for the neural arch. The cross-sectional shape of the first one is triangular, with a prominent ventral constriction. Dorsally the diapophyses contact the platform for the articulation of the neural arches and the anterior side of the vertebra. Parapophysis is fused with the posterior edge of the centrum and located just dorsal to the middle of its height. A narrow ridge connects both rib facets.

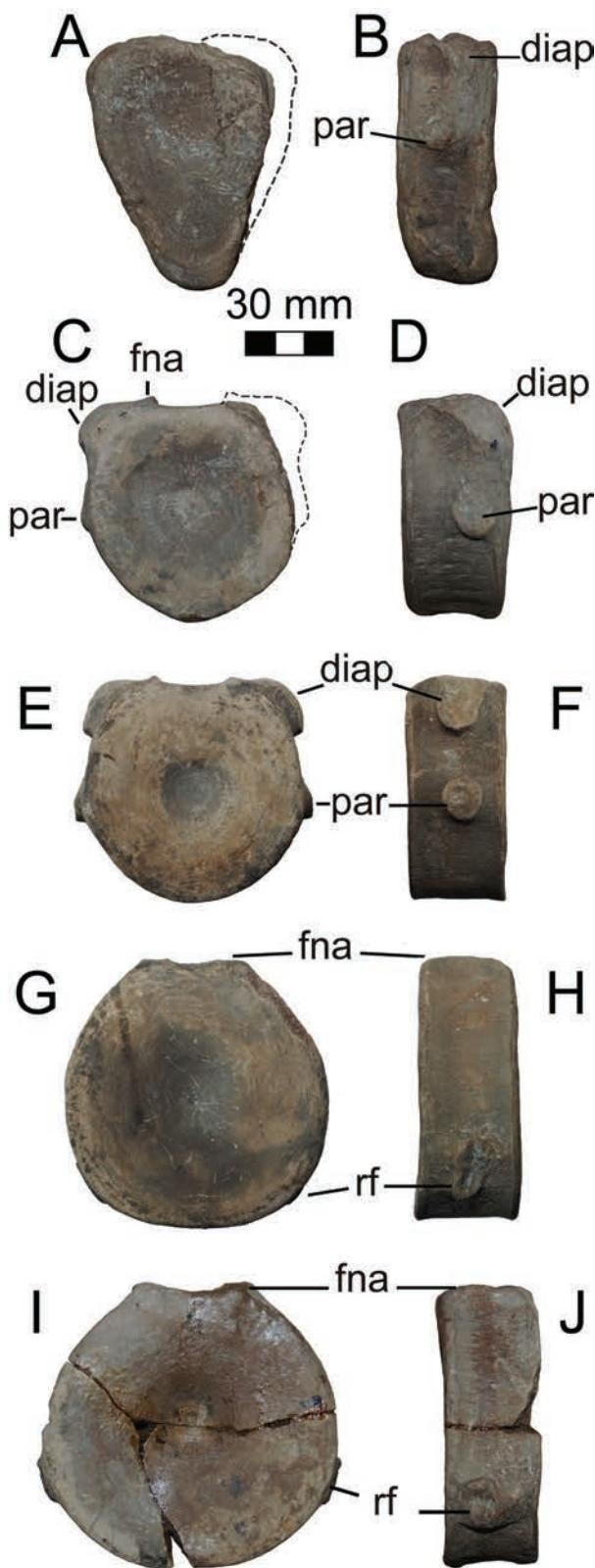
The second vertebra has a rounded cross-sectional outline and tapers slightly towards the ventral part (Fig. 5C, D). It demonstrates triangular facets for intercentra on its anterior and posterior edges in ventral view. Both rib facets are fused with the anterior edge of the centrum. The diapophyses are confluent with the facets for the neural arch.

The latter available anterior trunk centrum bears diapophysis fused with the neural arch and parapophysis located in the middle of the lateral surfaces of the centrum. The diapophysis does not contact the anterior edge of the centrum.

The available posterior trunk or anterior caudal centrum is rounded in outline and slightly tapering dorsally. It bears a single dorsoventrally elongated rib facet that demonstrates a coalescence of diapophysis and parapophysis.

The available caudal vertebra is rounded in cross-section. It bears a single rib facet shifted about two-thirds down the lateral surfaces of the centrum (Fig. 5E, F).

Scapula. The ventral part of the scapula is slightly anteroposteriorly expanded, 'S' – shape curved in medial view, and bears a rugose coracoid and glenoid



articular surface (Fig. 6A, B). The glenoid contribution of the scapula is reduced, being smaller than the coracoid facet (Fig. 6C). The acromion process is partially broken, but has probably been large, judging by the width of the broken surface. The acromion is not separated from the coracoid facet (Fig. 6C). The shaft is oval in cross-section at its midpoint. The anterior edge of the scapula is laterally flattened and bears a prominent area for the articulation with the clavicle (Fig. 6B).

Humerus. The humerus is not completely preserved since it misses the proximal end. It is dorsoventrally flattened, noticeably along its posterior side. Judged by the small angle between the long axes of the distal epiphysis and the diaphysis, the humeral “torsion” (the angle between the long axes of the proximal and distal ends of the humerus; see Kirton, 1983) is extremely reduced. On the dorsal surface of the humerus there is a marked, flattened dorsal process, extending obliquely forward to midschaft. The deltopectoral crest is poorly developed. It is located near the anterior margin of the anteroventral surface of the humerus. The distal end bears three oval facets for the preaxial accessory element, radius and ulna (Fig. 7D). The facet for the preaxial accessory element is flat. The articular surfaces for the radius and ulna are deeply concave and have a rugose surface. The ridge separates the ulnar facet from the radial facet. Torsion of the ulnar facet is pronounced (it is rotated slightly proximoventrally, and has a smaller width than the radial facet). The large muscle tubercles are pronounced on the dorsal and ventral surfaces near the ulnar facet (Fig. 7A, B).

Comparison. The genus *Arthropterygius* includes the remains of ichthyosaurs from two distant localities. The type species *A. chrisorum* was found in Arctic Canada (Russell 1993). An additional specimen (MOZ 6145) referred to as *Arthropterygius* sp. was described from Argentinean Patagonia (Fernández and Maxwell 2012). It should be noted that *Janusaurus lundi* recently described from Middle Volgian de-

Fig. 5. Vertebral centra of *Arthropterygius* sp. (SGM 1502): A, B – one of the first anterior trunk centrum in anterior (A) and left lateral (B) views; C, D – anterior trunk centrum in anterior (C) and left lateral (D) views; E, F – middle anterior trunk centrum in anterior (E) and left lateral (F) views; posterior trunk centrum in anterior (G) and right lateral (H) views; anterior caudal centrum in anterior (I) and right lateral (J) views. Abbreviations: diap – diaphysis; fna – facet for neural arch; par – parapophysis; rf – single rib facet.

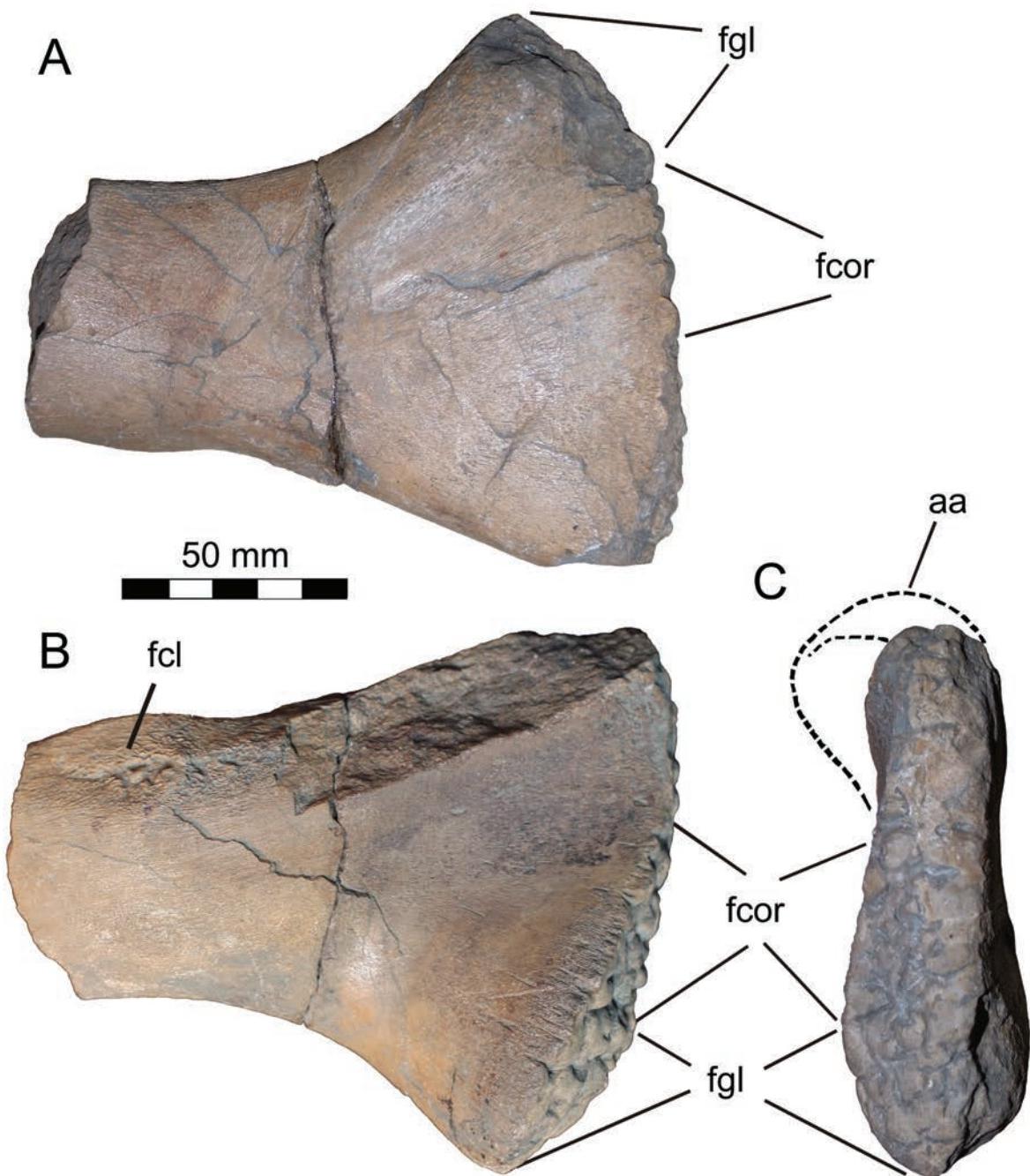


Fig. 6. Right scapula of *Arthropterygius* sp. (SGM 1502) in dorsoventral (A), lateroventral (B), and medial (C) views. Abbreviations: aa – acromion; fgl – glenoid contribution; fcl – facet for clavicle; fcov – coracoid facet.

posits of Svalbard (Roberts et al. 2014) also shares a number of diagnostic features with those of the genus *Arthropterygius* (e.g. extremely reduced extracondylar area of basioccipital, extremely reduced and shifted anteriorly deltopectoral crest, reduced humeral

torsion and strongly flattened posterior side of the humerus and pronounced torsion of the ulnar facet (Fernández and Maxwell 2012; Maxwell 2010)). It is therefore highly plausible that these two genera are very closely related and probably even synonymous.

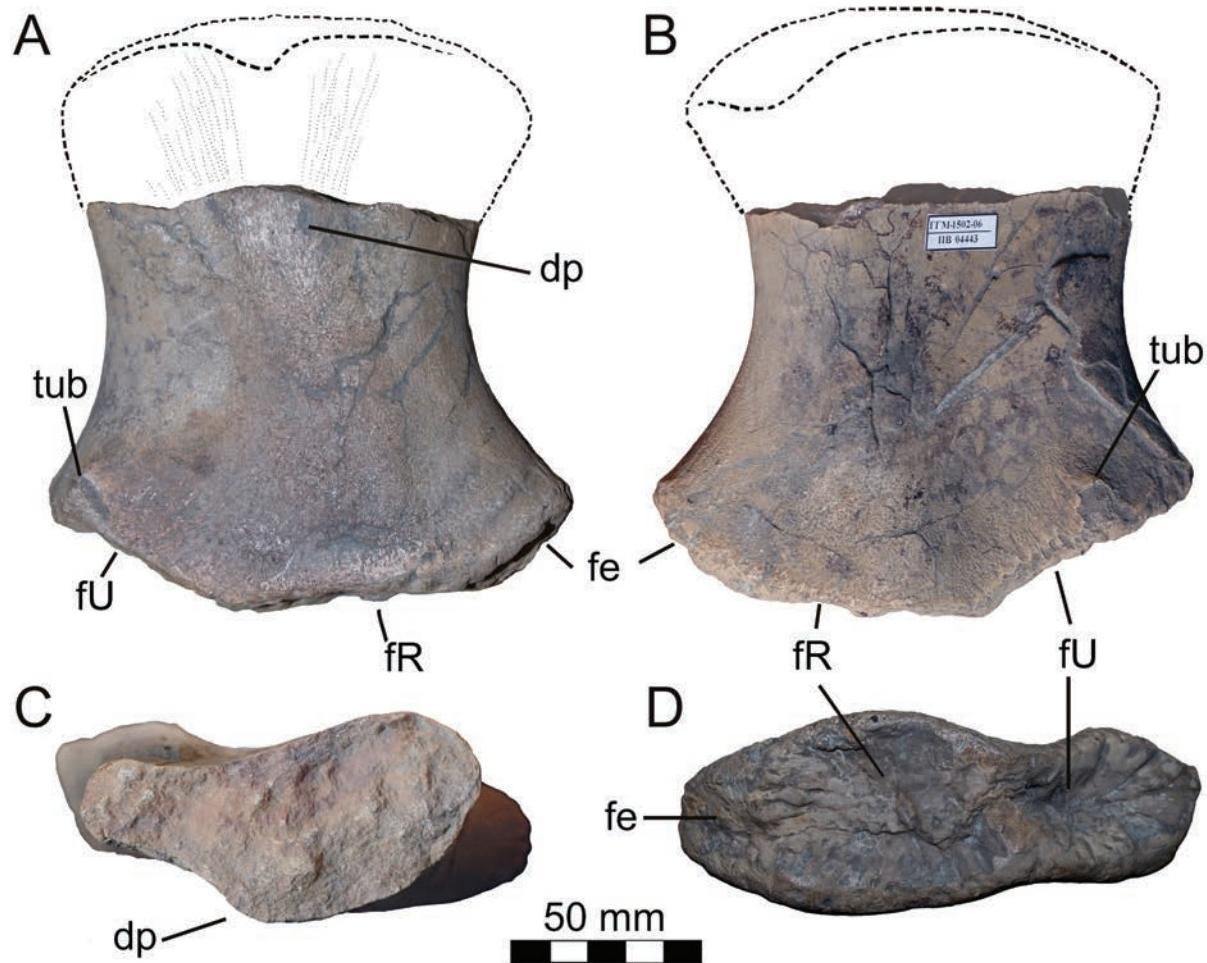


Fig. 7. Right humerus of *Arthropterygius* sp. (SGM 1502) in dorsal (A) ventral (B) views; diaphyseal section (C), and distal view (D). Abbreviations: dp – dorsal process; fe – facet for preaxial accessory element; fR – facet for radius; fU – facet for ulna; tub – tubercle.

However, due to the incompleteness of the specimens authentically referred to as *Arthropterygius* and the poor preservation of some significant elements in *Janusaurus* (e.g. basisphenoid) we considered the synonymisation to be premature.

The basisphenoid of MOZ 6145 is pentagonal in ventral view, while that of SGM 1502 is trapezoidal in outline. Unlike both of the previously described specimens referred to as *Arthropterygius*, SGM 1502 has no ledge between the foramen for the internal carotid artery and the ventral surface of the element. Furthermore, the SGM 1502 internal carotid foramen is restricted by the smooth edging at the top and at the sides. It has a rounded shape, unlike *A. chrisorum* and does not expand funnel-like as in MOZ 6145. SGM 1502 anterior foramen for the internal carotid

artery has a circular outline and large vessel diameter, thus it is different from the type species (Fernández and Maxwell 2012; Maxwell 2010).

Unlike *Arthropterygius chrisorum*, SGM 1502 has a more anteroposteriorly elongated distal humeral facets, resembling those described in *Janusaurus lundi*. Large and well pronounced muscular tubercles are present in SGM 1502. They are located on the dorsal and ventral surface near the ulnar facet, resembling those described in *Sveltonectes*, *Sisteronia* (Fischer et al. 2011, 2014b) and some individuals of *Ophthalmosaurus* (Andrews 1910; Kirton 1983; McGowan and Motani 2003). SGM 1502 has a peculiar feature – a compressed posterior part of the humerus, which is more similar to that of the Argentinian specimen and *J. lundi* as compared to *A. chrisorum*.

The ulnar facet in *Arthropterygius chrisorum* is not as wide as the radial facet, forming an abrupt drop of the humerus ventral surface. An ulnar facet:radial facet width ratio is 0.71 in *A. chrisorum* (Maxwell 2010), 0.77 in SGM 1502 and *Sisteronia seeleyi* (Fischer et al. 2014b), 0.8 in *J. lundi* (Roberts et al. 2014). In other Ophthalmosauridae this ratio tends to 1 (McGowan and Motani 2003).

All specimens differ in size: the total length of the humerus in *A. chrisorum* is 220 mm. Its length reaches 148 mm in MOZ 6145, 152 mm in *J. lundi* and it was approximately 160 mm in SGM 1502, according to its proportions. The length of the basisphenoid is at least 78 mm in *A. chrisorum*; near 70 mm in MOZ 6145 and 80 mm in SGM 1502.

The tooth morphology in SGM 1502 is most similar to the species of the subfamily Ophthalmosaurinae. The teeth in SGM 1502 are similar to those of *Ophthalmosaurus natans* (Gilmore 1902, 1905), having smooth roots with rounded cross-section and crowns ornamented by delicate longitudinal striae, which weaken to the apex of the tooth. The crowns of *Ophthalmosaurus icenicus* (Kirton 1983) show similar morphology to SGM 1502. Below the crown there is likewise a smooth area of acellular cementum, but in *O. icenicus* there is a well-pronounced thickening at the base of the acellular cementum area. The crowns in SGM 1502 are very similar to those of *Acamptonectes densus* (Fischer et al. 2012) especially by their slightly bulbous bases, which are more pronounced in *Acamptonectes*.

Only fragmentary scapulae are known in *Arthropterygius chrisorum* (Maxwell 2010). In SGM 1502 the scapula is characterized by a reduced glenoid contribution as in *Ophthalmosaurus icenicus* (Andrews 1910) *Platypterygius americanus* (Maxwell and Kear 2010), *Sveltonectes insolitus* (Fischer et al. 2011) and *Undorosaurus gorodischensis* (Efimov 1999). The acromion is not separated from the coracoid facet by a notch. The bone in the middle section of the scapular medial end was opposed in life to the anterior coracoid notch. It is not ossified in SGM 1502 as in some specimens of *Ophthalmosaurus* (Andrews 1910; Kirton 1983). The scapular medial notches are also absent in *U. gorodischensis* (Efimov 1999).

Remarks. The ventral surface of the SGM 1502 basisphenoid bears slight scratches and conical holes (Fig. 3A, B), which might be the traces of scavenger teeth. Obviously, the corpse was exhibited at the bottom surface long enough to be exposed for scavengers.

Subfamily Ophthalmosaurinae Baur, 1887 *sensu* Fischer et al., 2012

Genus *Ophthalmosaurus* Seeley, 1874

Ophthalmosaurus sp.

Referred material. IG KSC 415/38 incomplete right forefin.

Locality and horizon. Polar District of Nenets Autonomous Region (Okrug), Volonga River, 7 km above the mouth within the Volonga detached mass (Fig. 1); Upper Volgian to Berriassian.

Description. Measurements taken on IG KSC-415/38 can be found in Table 1.

The humerus is not completely preserved since the proximal portion is missing. It seems that a strong dorsal process extended towards the radial facet. A portion of the prominent deltopectoral crest extends anteriorly to the radial facet. Three distal articular facets for preaxial element, radius and ulna are present. The facet for the preaxial accessory element corresponds at the anteriormost one. It is slightly concave and subtriangular in shape. The radial and ulnar facets are deeply concave, rounded in outlines and they have a rugose surface (Fig. 8G). A ridge separates the ulnar facet from the radial facet.

Three epipodial elements articulate with the humerus (Fig. 8A). Only the posterior part of the preaxial accessory element is preserved. The radius has a pentagonal outline and articulates anteriorly with the preaxial accessory element, anterodistally with the radiale, posterodistally with the intermedium, posteriorly with the ulna. Of the latter on the proximal part is preserved. Judging by the fragment, it seems to have been larger than the radius. The proximal surfaces of both epipodials are rugose, convex and deeply fit into the concave facets of the humerus (Fig. 8D, E). The posterior edge of the ulna appears to taper posteriorly, which is an ophthalmosaurinae synapomorphy. The distal portions of the radiale and the intermedium are missing.

DISCUSSION

In general, the morphology of the material from the Nenets Autonomous Region is similar to that of *Ophthalmosaurus icenicus* as compared to any other ophthalmosaurid, having deeply concave facets, the triangular facet for the preaxial accessory element (Andrews 1910; Kirton 1983); there is no promi-

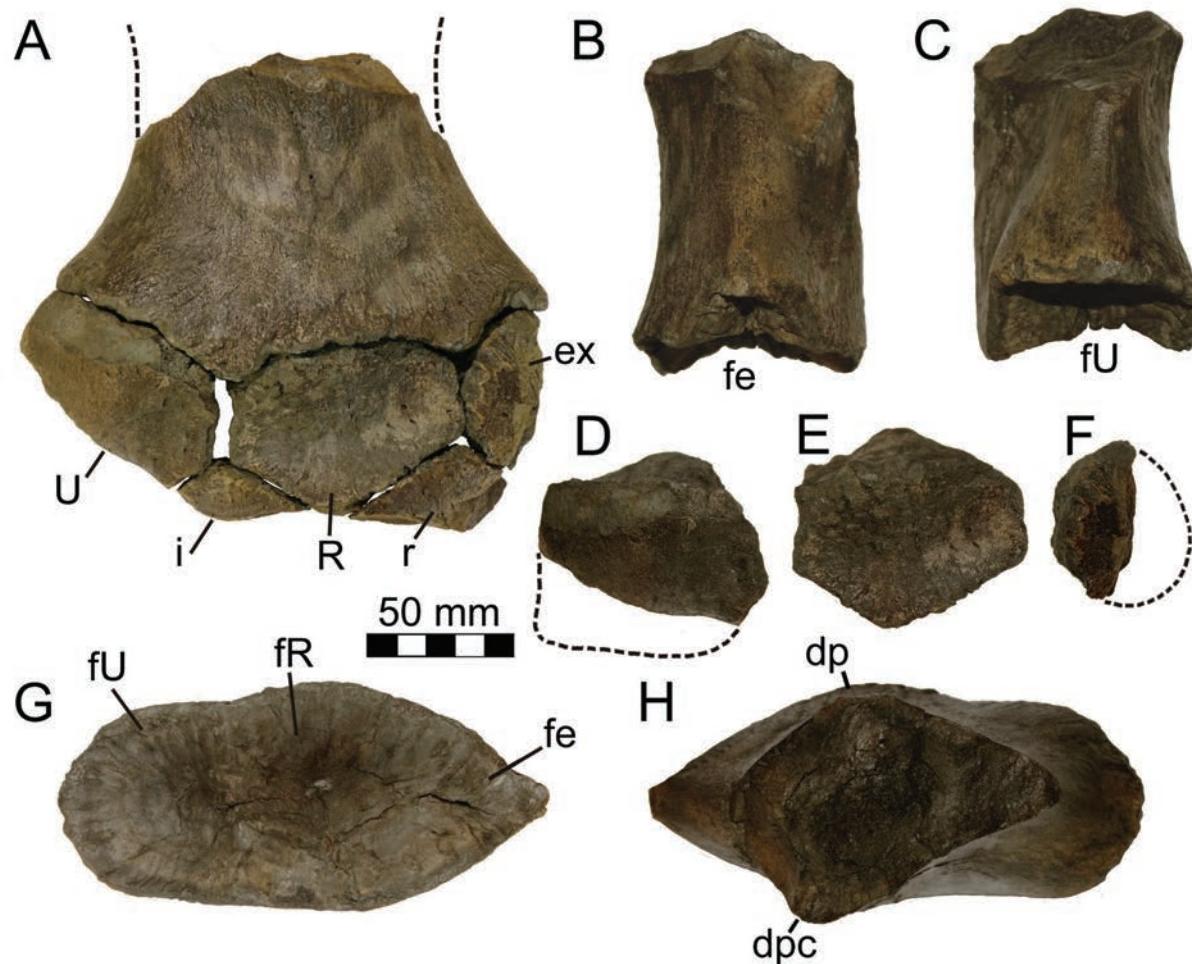


Fig. 8. Partial right forefin of *Ophthalmosaurus* sp. Seeley, 1874 (IG KSC-415/38): A – dorsal view; B – humerus in anterior view; C – humerus in posterior view; D – ulna in dorsal view; E – radius in dorsal view; F – preaxial accessory element in dorsal view; G – humerus in distal view; H – section through the diaphysis. Abbreviations: dp – dorsal process; dpc – deltopectoral crest; fe – facet for preaxial accessory element; fR – facet for radius; fU – facet for ulna; H – humerus; i – intermedium; R – radius; r – radiale; U – ulna; x – preaxial accessory element.

nent posterior torsion of the ulnar facet. Therefore, IG KSC-415/38 has been tentatively assigned as *Ophthalmosaurus* sp.

Distinctive features of IG KSC-415/38 are the convex proximal surfaces of the radius and ulna, which fit the facets of the humerus, making them similar to *Arthropterygius* (Maxwell 2010). Such “peg-in-socket” articulation of the epipodial bones with the humerus, appears to be fairly common among both the platypterygiinae (Broili 1907; Fischer et. al. 2011) and the ophthalmosaurinae (Kirton 1983) ophthalmosaurids, most prominent in *Arthropterygius* (Maxwell 2010). However, most researchers

have not paid sufficient attention to this feature. Apparently, it is due to the fact that the limb elements are frequently in articulation and their contacts are not clearly visible.

Our previous knowledge of *Arthropterygius* is based on the descriptions of two incomplete specimens from the Oxfordian to Kimmeridgian Ringnes Formation, Canada and the Tithonian of the Vaca Muerta Formation in Argentina. The material from the Komi Republic of Russia provides new anatomical information for the genus and demonstrates that *Arthropterygius* was more diverse than previously thought.

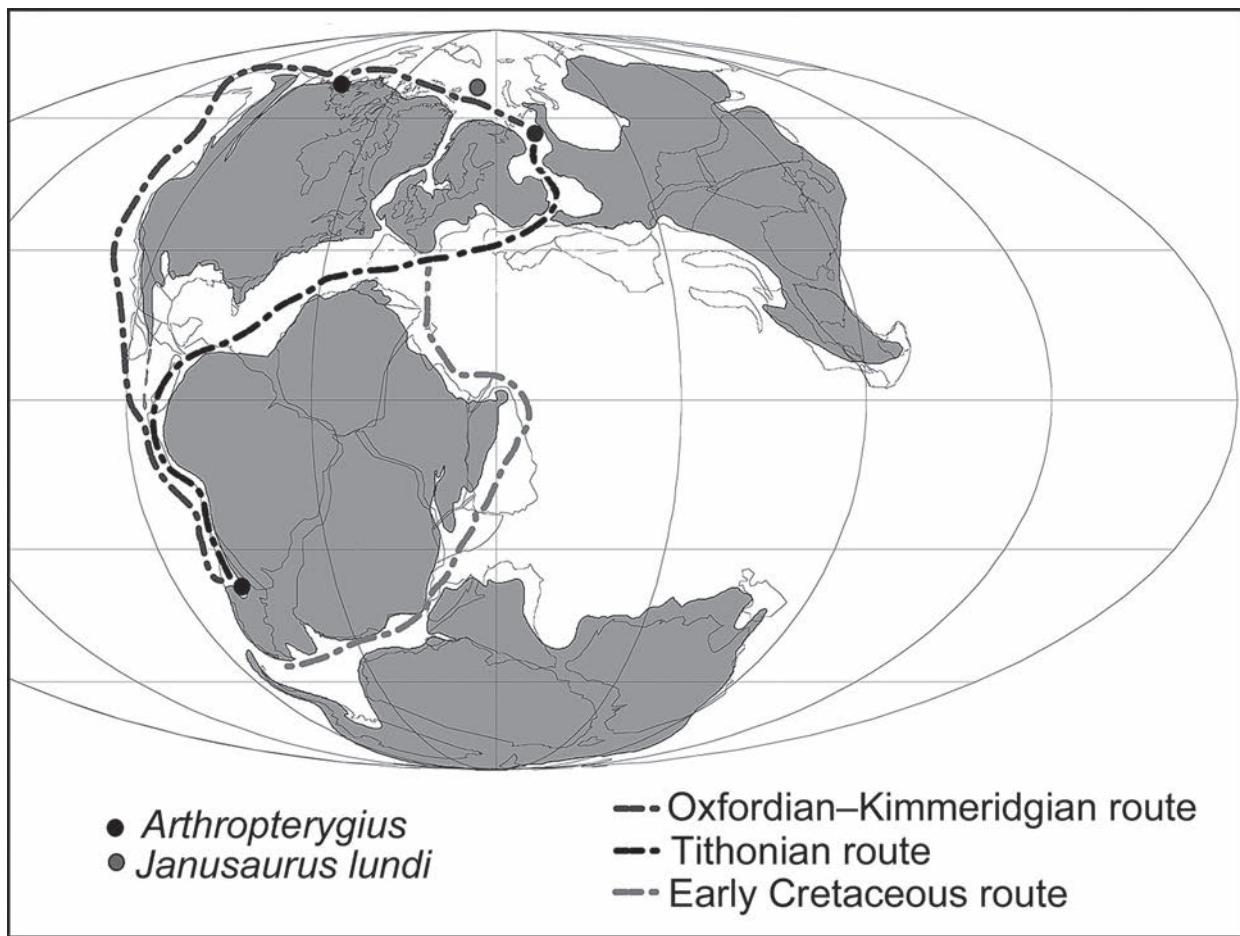


Fig. 9. Palaeobiogeographical scheme of ichthyosaurs distribution during the Late Jurassic (Tithonian/Volgian) – Cretaceous showing the occurrences and possible migration routes of the genus *Arthropterygius*. Map modified from Rees et al. (2000).

Russian ichthyosaur remains from Lower and Upper Cretaceous deposits are very abundant and diverse. This diversity has been demonstrated in the recent years, and new species have been assigned (*Platypterygius ochevi* Arkhangelsky et al., 2008; *Sveltonectes insolitus* Fischer et al., 2011 and *Leninia stellans* Fischer et al., 2014a). And the Jurassic specimens have been reported in the Volgian localities of Saratov, Ulyanovsk and Moscow regions. The representatives are *Paraophthalmosaurus saveljeviensis* Arkhangelsky, 1997, *Undorosaurus gorodischensis* Efimov, 1999 and *U. trautscholdi* Arkhangelsky et Zverkov, 2014, “*Otschevia*” *pseudoscythica* Efimov, 1998, “*O.*” *zhuravlevi* Arkhangelsky, 1997 and “*O.*” *alekseevi* Arkhangelsky, 2001. Nevertheless, for a few years these specimens have been considered to be synonyms of *Ophthalmosaurus* and *Brachypterygius*

(Maisch and Matzke 2000; McGowan and Motani 2003), without a detailed comparative study of their remains.

The ichthyosaurs from Komi Republic and Nenets Autonomous Region demonstrate that the diversity of ophthalmosaurid ichthyosaurs was still high at high latitudes in the northern hemisphere at the end of the Tithonian (Volgian) (Fig. 9). Examples of this diversity have been reported in the Volgian of Svalbard, Norway (Druckenmiller et al. 2012; Roberts et al. 2014) with *Cryopterygius kristiansenae*, *Palvennia hoybergeti* and *Janusaurus lundi*. It has been increasingly demonstrated that ophthalmosaurid ichthyosaurs crossed the Jurassic/Cretaceous boundary and that their diversity remained high until the Upper Cretaceous, prior to their extinction (Fischer et al. 2012, 2014b).

The distribution of *Arthropterygius* appears to be restricted to the cold waters at high latitudes. However, new studies are required to verify this assumption. We have no evidence of behavioral strategies such as seasonal migrations of ichthyosaurs across the globe. And if migrations occurred, we still cannot define the exact sea routes and the directions they followed. Nevertheless, ichthyosaurs having been able to swim pelagically; the opportunistic prey capture and the ovoviparous form of reproduction caused their dispersion in the Jurassic (Gasparini and Fernández 1997). The outcrops of Russia, Canada, Argentina and Norway where *Arthropterygius* and *Janusaurus lundi* have been reported, allow us to develop a hypothesis concerning the possible migratory/dispersal routes (Fig. 9).

The first route appeared to run along the Eastern Pacific currents during the Oxfordian to Kimmeridgian, as was previously discussed by Fernández and Maxwell (2012) and through the boreal zone in the northern hemisphere, while the Hispanic Corridor was not completely functional (Stanley 1994). During the Late Jurassic the continental drift of Gondwana and consecutive marine transgression opened new dispersal routes for pelagic reptiles (Gasparini and Fernández 1997). During the Tithonian, the already operative Hispanic Corridor could have caused the interchange of fauna between the Eastern Pacific and the Western Tethys (Damborenea and Manceñido 1979; Gasparini 1992; Gasparini and Spatelli 1993; Gasparini and Iturrealde-Vinent 2006). The findings in Canada, Norway, Russia and Argentina support this hypothesis.

A third dispersal seaway might have helped the faunal exchange between Western Tethys and the Eastern Pacific, through a shallow epicontinental seaway, which connected with East Africa and the Southern Patagonia. This southern route might have opened during the Late Tithonian to the Berriassian and has been analyzed by a number of authors, who have given it different names (the 'Trans-Erythraean Seaway'; 'South Africa/Rocas Verdes seaway', or 'Indo-Madagascan sea-way'; Arkell 1956; Cecca 1999; Schultz et al. 2003; Hikuroa 2008; Salazar 2012). Nevertheless, the morphological similarity between the specimens in Russia, the UK, Norway and Southern Patagonia indicates that this migration had not occurred until the Early Cretaceous, when the corridor was completely opened (Pardo Pérez et al. 2012; Stinnesbeck et al. 2014 and unpublished data).

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APPENDIX 1

Determination of stratigraphic range of specimens

Arthroptyrgius sp. (SGM 1502)

E.M. Tesakova (Lomonosov Moscow State University) has determined the presence of ostracods *Galliaeicytheridea mandelstami* (Lübitzova, 1955) and *Mandelstamia ventrocornuta* (Sharapova, 1939)

characterizing Galliaeicytheridea – Macrodentina (Polydentina) ramosa ostracod Zone (Lower Volgian) and Cytherella – Reticlythere cornularialis ostracod Zone (Middle Volgian). According to the stratigraphic charts (Kolpenskaya 1999; Mitta et al. 2012; Tesakova 2014), both species are common in the Lower and Middle Volgian deposits of the East European Platform.

M.A. Ustinova (GIN RAS) has established the following assemblage of foraminifera: *Dentalina* sp., *Astacolus declavatus* Bassov, *Lenticulina kovalevskyi* Dain, *Citharina* sp., *Marginulina impropria* Bassov, *Planularia bicostata* Ivanova, *Saracenaria pravoslavlevi* (Furssenko et Poljenova). These species are common in the Middle Volgian and is highly possible to assign the studied sample to the *Dorsoplanites panderi* Zone.

According to G.N. Alexandrova (Geological Institute of RAS) the dinoflagellate cysts are poorly preserved. Their assemblage is typical for the Jurassic and is represented by smooth *Chytroesphaeridia* and tiny-spined *?Trichodinium* as well as by the fragments of *Polystephanophorus*. The latter occurs above the Bathonian Stage only. Thus, dinoflagellate assemblage confirms the Upper Jurassic age of the deposits.

Ophthalmosaurus sp. (IG KSC-415/38)

According to the analysis conducted by L.A. Selkova (IG KSC UB RAS) macerate obtained after treatment with a standard methodology for palynological analysis contains a large amount of small rounded and teardrop-shaped coal particles making it difficult to detect certain forms. Discovered microphytobenthos of poor preservation are crumpled and torn, so it is impossible to hold the definition of species. Among microphytobenthos dinoflagellate cysts, acritarchs, prasinophytes, spores and pollen of terrestrial plants are presented. The largest percentage of dinocysts are defined: *Gonyaulacysta* with species *G. eisenackii* (Defl.), *G. jurassica* (Defl.) Nor. et Sarj. subsp. *adecta* Sarj., *G. jurassica* (Defl.) Nor. et Sar. subsp. *jurassica* Gorka, *Gonyaulacysta jurassica* (Defl.) Nor. et Sarj. subsp. *adecta* Sarj. var. *longicornis* (Defl.) Sarj., *Gonyaulacysta* sp., *Rhynchodiniopsis* sp., *R. martonense* Bailey et al., *Cribroperidinium* sp., *C. mudergonense* (Cook et Eisen.) Davey, *Lithodinia* sp., *Paragonyaulacysta* sp., *Scriniodinium crystallinum* (Defl.) Klement, *Sirmiodinium grossii* Alb., *Kalyphea* sp., *Prolixosphaeridium* sp.,

Cleistosphaeridium sp., *Circulodinium* sp., *Chlamidophorella* sp., *Chytroeisphaeridia* sp., *Tubotuberella rhombiformis* Vozzen, *Pareodinia prolongata* Sarj., *Gochteodina villosa* Vozz., *Occisucysta* sp., *Valvaeodinium* sp., *Heslertonia* sp. A large number of chorate forms were found: *Systematophora* sp., *S. aff. daveyi* Riding et Thomas, *Olygospshaeridium* sp., *O. complex* (White) Davey et Williams, *Perisseiasphaeridium* sp., *Adnatosphaeridium* aff. *caulleryi* (Defl.) Woll. et Down. Forms, whose appearance is marked in Early Cretaceous – *Leberidocysta* sp., *Aptea anaphrissa* (Sarj.) Sarj. et Stover. Single acritarchs (*Micrhys tridium* sp.) and parasinophytes (*Pterospermella* sp.) are present.

A small amount of spores and pollen of terrestrial plants were detected: *Cyathidites australis* (Coup.), *Gleicheniidites angulata* (Naum.), *G. laetus* (Bolch.), *G. senonicus* (Ross), *G. triplex* (Bolch.), *Osmundac idites jurassicus* (K.-M.), *Piceapollenites* sp., *Classopol lis classoides* (Pflug), *Sciadopityspollenites mesozoicus* Coup., *Ginkgocycadophytus* sp.

A large number of small forms of foraminifera *Microforaminifera* sp. were found.

We can assume that the set of forms encountered on the Volgian age, but the presence of the Cretaceous forms (*Leberidocysta* sp., *Aptea anaphrissa* (Sarj.) Sarj. et Stover) makes precise age determination problematic.